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Abstract: Intensification of agriculture and associated loss of habitat heterogeneity is a key driver of global declines in insect pollinators. Pollinators utilise different habitats to meet resource requirements throughout their life-span and it is widely accepted that their conservation requires a landscape-scale approach. Information on the mechanisms driving insect pollinators at the landscape scale is, however, lacking. To fill this knowledge gap, this novel study explores how pollinators utilise different habitats within a landscape and how utilisation changes over the season. Floral resources and insect pollinators (i.e. bumblebee, butterflies and hoverflies) were monitored during peak pollinator activity periods on a wide range of agricultural and semi-natural habitats in an intensive grassland landscape.
The availability of key foraging resources differed between semi-natural habitats and this was strongly linked to their utilisation by pollinators. Floral resources were most abundant and diverse in road verges, riparian buffer strips and open scrub. These were key habitats for butterflies, with road verges and buffer strips also being important for hoverflies and bumblebees. The relative value of semi-natural habitats in providing floral resources changed throughout the season. Pollinators appeared to respond to changes in key floral resources, dynamically using different semi-natural habitats to meet their requirements. Maintaining landscape heterogeneity and improving the quality of semi-natural habitats to ensure resource diversity and continuity is fundamental to pollinator conservation. Regionally targeting agri-environment spending could result in the simplification of agricultural landscapes with consequences on insect pollinators and biodiversity as a whole.

Graphical Abstract

Increases the diversity of resources available and thus enables a greater diversity of pollinator species to be supported

Provides resources at different points in time thus increasing the temporal stability of resources at the landscape level

Landscape Diversity

Provides the different resources that a species requires at a single point in time (e.g. pollen and nectar)

Provides resources required during different life-cycle stages (e.g. caterpillar food plants and adult nectaring sites)

Highlights

- The role different habitats play in providing resources for pollinators is explored.
- Road verges and riparian buffer strips provided key floral resources for pollinators.
- Different habitats have the potential to increase the diversity of floral resources.
- Different habitats have the potential to stabilise the availability of floral resources.
- Pollinators use different habitats to meet resource requirements through the season.

Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape

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Abstract

Intensification of agriculture and associated loss of habitat heterogeneity is a key driver of global declines in insect pollinators. Pollinators utilise different habitats to meet resource requirements throughout their life-span and it is widely accepted that their conservation requires a landscape-scale approach. Information on the mechanisms driving insect pollinators at the landscape scale is, however, lacking. To fill this knowledge gap, this novel study explores how pollinators utilise different habitats within a landscape and how utilisation changes over the season. Floral resources and insect pollinators (i.e. bumblebee, butterflies and hoverflies) were monitored during peak pollinator activity periods on a wide range of agricultural and semi-natural habitats in an intensive grassland landscape.

The availability of key foraging resources differed between semi-natural habitats and this was strongly linked to their utilisation by pollinators. Floral resources were most abundant and diverse in road verges, riparian buffer strips and open scrub. These were key habitats for butterflies, with road verges and buffer strips also being important for hoverflies and bumblebees. The relative value of semi-natural habitats in providing floral resources changed throughout the season. Pollinators appeared to respond to changes in key floral resources, dynamically using different semi-natural habitats to meet their requirements. Maintaining landscape heterogeneity and improving the quality of semi-natural habitats to ensure resource diversity and continuity is fundamental to pollinator conservation. Regionally targeting agri-environment spending could result in the simplification of agricultural landscapes with consequences on insect pollinators and biodiversity as a whole.

Key words: Agri-environment schemes, pollination, ecosystem services, biodiversity, landscape diversity, floral resources

1. Introduction

Agricultural intensification, loss of (semi-) natural habitat and associated decline of floral resources are primary factors driving global declines in wild insect pollinators (Baude et al., 2016; Vanbergen and The Insect Pollinators Initiative, 2013). Strong links between biodiversity and ecosystem functioning exist; maintaining biodiversity is key to the delivery, stability and resilience of ecosystem services many of which are vital to agricultural production (Bai et al., 2004; Tilman et al., 2014). Insect pollination is critical in preserving terrestrial ecosystems (Ollerton et al., 2011); with insect pollinators enhancing yields in approximately 70% of crops their value to agriculture is indisputable (Klein et al., 2007). With demand for pollinator-dependant crops rising at the same time as pollinators are declining, there are concerns that this imbalance could result in a pollination deficit adversely impacting on global food security (Aizen et al., 2009). Enhancing pollinator diversity can increase pollination success due to functional and temporal complementarity between species (Blüthgen & Klein, 2011; Albrecht et al., 2012) and can increase the stability and resilience of pollination through a variety of stabilising mechanisms. Such mechanisms include inter-specific differences in response to environmental change (i.e. response diversity); increased chance that some species will adapt to change; and inter-specific differences in response to a specific environmental factor across spatial or temporal scales (i.e. cross-scale resilience) (Garibaldi et al., 2014; Winfree, 2013).

Extensive research has evaluated specific habitat components (e.g. agricultural and (semi-) natural) and the impact of habitat quality, management and agri-environment interventions on pollinators (Haaland et al., 2011; Noordijk et al., 2009; Pywell et al., 2011; Williams et al., 2012). Within agricultural landscapes such habitats do not exist

in isolation but within a matrix of farmed and semi-natural habitats; landscape structure has been identified as a key driver of pollinator diversity (Garibaldi et al., 2011; Scheper et al., 2013). Studies investigating the impact of landscape structure on pollinators, and the delivery of pollination services, typically utilise broad scale measures of landscape complexity such as proximity to, or area of, (semi-) natural habitat (Garibaldi et al., 2011; Klein et al., 2012; Scheper et al., 2013) and indices of landscape diversity (Petersen and Nault, 2014). Such studies highlight the importance of (semi-) natural habitat components on pollinators and pollination success (Garibaldi et al., 2014; Klein et al., 2012; Petersen and Nault, 2014). Many wild pollinators are highly mobile utilising local and landscape scale cues when foraging (Jha & Kremen, 2013). Positive impacts of landscape diversity may therefore be expected as a result of different habitats supporting differences in pollinator resource requirements both spatially and temporally; enhancing resource diversity and stability (Blüthgen and Klein, 2011; Shackelford et al., 2013; Williams et al., 2012).

Insect pollinators utilise different habitats to meet resource requirements throughout the season (Mandelik et al., 2012; Williams et al., 2012). Studies that simultaneously determine the value of different habitat components for pollinators, or how utilisation changes over time, are however rare focussing on a narrow subset of habitats (Mandelik et al., 2012) or species (Williams et al., 2012). Research at large spatiotemporal scales is critical to understand the processes driving pollinator populations at the landscape scale. Such knowledge is fundamental to the development of landscape-scale pollinator conservation initiatives. Focussing on an intensive agricultural landscape, this study determines the relative value of a broad

range of habitats in the provisioning of floral resources for insect pollinators (i.e. bumblebees, butterflies and hoverflies) and explores how this changes over the season. The relationship between resource availability and the utilisation of habitats by insect pollinators, and seasonal changes in this utilisation, is explored. A combination of statistical modelling and observational evidence provide insight into the mechanisms driving pollinator assemblages at the landscape scale and are used to explore the concept that pollinators move between habitats in response to resource availability (Fig. 1). Research findings will increase our understanding of how landscape structure and composition influences resource provisioning and resource stability.

2. Methods

2.1. Study sites

The study was conducted in the Cessnock Water catchment Ayrshire, Scotland (N55°32′50″, W4°22′00″). This 75.9 km^2 catchment is dominated by productive ryegrass, *Lolium perenne* L., swards primarily grazed by livestock and/or cut for silage. Twelve habitats that were either dominant within the catchment, or considered to be potentially important for insect pollinators were investigated: Arable, Intensive Grassland, Rough Grassland, Open Scrub, Riparian Buffer Strips, Coniferous Woods, Coniferous Wood Edges, Deciduous Woods, Deciduous Wood Edges, Intact Hedges (hedges with no gaps over 2 m), Sparse Hedges (hedges with gaps over 4 m) and Road Verges (Table 1, Fig. A.1). To minimise the impact of adjacent habitats, woodland edges, hedges, and buffer strips were selected adjacent to intensive grassland or arable fields.

In 2013, a total of 60 sites were surveyed (i.e. five sites per habitat class). In 2014, 24 of these sites (i.e. two per habitat class) were resurveyed and 24 sites (i.e. two per habitat class) new to the study were also surveyed (i.e. 48 sites in total). This gave a total of 84 sites (i.e. seven unique sites per habitat) over the two year period. Sites occurred on 35 farms and were selected to maximise spatial spread within a habitat class (i.e. minimum distance between sites in a habitat class was 904.2 m in a specific year: Fig. 2). This helped ensure independence between replicates within a habitat class (i.e. limited overlap of pollinator foraging area). As this study intended to explore the idea that pollinators move between habitats in response to their relative profitability it was not necessary to ensure that different habitats were independent. The minimum distance between different habitats was therefore approximately 25 m (i.e. for woodlands and their adjacent woodland edge).

2.2. Insect pollinator and botanical sampling

Three taxa of pollinators that all depend strongly on floral resources as adults were surveyed: butterflies, bumblebees and hoverflies. Additional resource requirements, however, differ due to differences in ecology and life-history. Most bumblebees observed were social species and therefore central placed foragers that return to their nests between foraging visits. Butterflies require shelter as adults and larval food plants that show considerable interspecific variation. Hoverfly larvae have extensive interspecific variation in resource requirements with insectivorous, phytophagous, saprophagous and coprophagous larvae all being represented (Stubbs and Falk 2002).

Insect pollinators and flowering plants were monitored by standardised transect walks under conditions stipulated by the Butterfly Monitoring Scheme Standards (i.e. temperature 13–17^{o}C with at least 60% clear sky, or over 17^{o}C if cloudy, not raining, maximum wind speed of Beaufort Scale 5: Polland and Yates, 1993). To standardise sampling effort all transects were walked at a constant rate of approximately 10 m min^{-1}. Monitoring was conducted over four sampling periods annually: June (12th – 20th June), July (9th – 13th July), early August (28th July – 4th August) and late August (18th – 23rd August).

All butterflies, foraging bumblebees, foraging hoverflies and plants observed in flower within the transect area were identified to species level and quantified. Flower abundance was quantified using the Domin Scale converted to percentage cover prior to statistical analyses (Currall, 1987). Plant-pollinator interactions were recorded by documenting the plant species pollinators were observed foraging on. Hoverflies observed foraging in the transect area were netted and identified in the laboratory following Stubbs and Falk (2002) and Speight and Sarthou (2012). A total of nine bumblebee species were observed consisting of the six most common UK social bumblebees and three cuckoo bumblebees (Table A.1). Due to difficulties in differentiating between workers of *Bombus lucorum senso lato* (i.e. species complex of *Bombus lucorum, Bombus cryptarum* and *Bombus magnus*) and workers of *Bombus terrestris* based on morphological features, analyses were conducted on the aggregated data for these species (Wolf et al., 2010). Most bumblebees were thus readily identifiable in the field (Potts et al., 2009) with difficult specimens being brought back to the laboratory (Prys-Jones and Corbet, 1991).

Permanent transects were established at all sites to ensure consistency in survey area between sampling dates (and sampling year for sites sampled in both years). Transects in nonlinear habitats (i.e. Arable, Intensive Grassland, Rough Grassland, Open Scrub, Coniferous Woods and Deciduous Woods) were 100 m in length and established in the habitat centre to avoid edge effects. Pollinators and flowering plants were monitored 2 m (1 m for hoverflies) on either side, and 2 m (1 m for hoverflies) in front, of the observer. Transects adjacent to linear features (i.e. Riparian Buffer Strips, Coniferous Wood Edges, Deciduous Wood Edges, Intact Hedges, Sparse Hedges and Road Verges) were established at a distance of two meters from the linear feature for bumblebees and one meter from the linear feature for hoverflies. Linear feature transects were 200 m long and 2 m (1 m for hoverflies) to one side, and 2 m (1 m for hoverflies) in front of the observer. The transect area for both linear and non-linear habitats was thus standardised (i.e. 400 m^2 for bumblebees, butterflies and plants in flower and 200 m^2 for hoverflies).

2.3. Analyses

2.3.1. Plant pollinator interactions

To detect temporal changes, plant-pollinator interaction data were summarised for each of the four *Sampling periods* (irrespective of *Habitat*). To determine how plant-pollinator interactions differed between habitats, data were summarised for each of the 12 *Habitats* (irrespective of *Sampling period*). Plant-pollinator interaction graphs were produced using the bipartite package (Dormann et al., 2009) in R (R Core Team, 2015).

2.3.2. Determining drivers of plant and pollinator communities

For plants in flower and for each of the three pollinator taxa separately (i.e. bumblebee, butterfly and hoverfly) three measures of community structure were calculated.

(i) Area or Abundance: percentage of the transect area consisting of inflorescences, the number of butterflies (i.e. irrespective of whether they were foraging), foraging bumblebees and foraging hoverflies.

(ii) Species richness: total number of species sampled.

(iii) Diversity: Shannon diversity index.

A number of Linear Mixed Models (LMMs) and Generalised Linear Mixed Models (GLMMs) were fitted using sequential tests to investigate the impact of *Habitat* and *Habitat* x *Sampling period* (i.e. to test if *Habitat effects* were consistent across *Sampling periods*) on the above response variables. For pollinator response variables the impact of floral resources (i.e. *Area of flowers* and *Flower species richness*) was explored by testing these variables both before and after *Habitat* (and *Habitat x Sampling period* for models including this fixed effect). This helped to determine if *Habitat* and *Habitat x Sampling period* effects could solely be attributed to differences in floral resources. All pollinator results were thus drawn from models with fixed effects tested in two orders (see below). To control for annual and seasonal variation, the fixed effects *Year*, *Sampling period* and *Year x Sampling period* were included in all models prior to the effects of interest.

Models were first fitted to the full data set to determine the impact of *Habitat* and, in the case of insect pollinators, floral resource variables (i.e. *Area of flowers* and *Flower species richness*):

flower response variables

- *Year* + *Sampling period* + *Year x Sampling period* + ***Habitat***

bumblebee, butterfly and hoverfly response variables

- *Year* + *Sampling period* + *Year* x *Sampling period* + ***Habitat + Area of flowers + Flower species richness***
- *Year* + *Sampling period* + *Year* x *Sampling period* + ***Area of flowers + Flower species richness + Habitat***

Bumblebees were never recorded in Arable sites and thus for bumblebees this *Habitat* class was omitted.

The above models were extended to include *Habitat* x *Sampling period* as a fixed effect - tested immediately following *Habitat.* Due to scarcity of pollinators in some habitats during specific sampling periods, it was not possible to fit these more complex models to the full data set so they were restricted to six key habitats (i.e. Rough Grassland, Open Scrub, Riparian Buffer Strips, Intact Hedges, Sparse Hedges and Road Verges).

For response variables based on counts (i.e. species richness and butterfly, bumblebee and hoverfly abundance) GLMMs were fitted in Genstat 16 using Residual Maximum Likelihood (REML), a log link function and assuming Poisson distributed errors. LMMs were fitted to all other response variables using REML. The data (after transformations if required) met the model assumptions. Approximate *F* tests were used to test fixed effects sequentially in the orders listed above, based on variance components estimated from the full models including all listed fixed effects. To determine where significant differences occurred, *post hoc* pairwise comparisons were made by including appropriate contrasts in fixed effects and using the false

discovery rate method to correct for multiple comparisons (Benjamini and Yekutieli, 2001).

Farm was included in all models as a random effect to take into account geographical variability (i.e. to allow that variability between transects on different farms is likely to be greater than variability between transects on the same farm). *Transect* and *Transect* x *Year* were also included as random effects to allow for repeated measures at a specific *Transect* (i.e. over different years and different sampling periods within a year). For LMMs the residual was *Sample* (i.e. data derived from a specific *Transect* on a specific *Sampling period* in a specific *Year*) and for GLMMs dispersion was estimated to allow for both over and under dispersal in response variables (McCullagh and Nelder 1989).

3. Results

3.1. Plant pollinator interactions

3.1.1. Overall trends

Over the study period 1,011 bumblebees (consisting of eight species), 740 butterflies (consisting of nine species; 255 actively foraging), and 985 hoverflies (consisting of 47 species) were recorded (Table A.1). 111 species of plants were observed in flower; pollinators were recorded on 68 of these species (Table A.2) yielding a total of 2,251 plant-pollinator interactions.

Of these interactions, 71.9% occurred on just ten flower species, in order of frequency: *Centaurea nigra*, *Cirsium arvense*, *Rubus fructicosus*, *Stachys palustris*, *Filipendula ulmaria*, *Ranunculus* repens, *Cirsium palustre*, *Succisa pratensis*,

Symphytum x uplandicum and *Angelica sylvestris*. Pollinators were typically generalists, and with the exception of a small number of rarely observed species, foraged on several flower species (Fig. A.2). Both the frequency of visits to specific flowers and the key flowers visited, however, differed between taxa. *Centaurea nigra*, *Cirsium spp.* and *R. fructicosus* were commonly visited by all three taxa. Bumblebees and hoverflies frequently visited *S. palustris* and *F. ulmaria;* hoverflies commonly visited *R. repens*, *A. sylvestris*, and *Leontodon* spp. with bumblebees commonly foraging on *Symphytum x uplandicum.* Flower species pollinators visited showed clear seasonal differences that were largely related to flowering period (Fig. A.2 and A.3). *Symphytum x uplandicum* and *R. repens* were important in June, *R. fructicosus*, *F. ulmaria*, *Heracleum sphondylium* and *C. arvense* in July and *C. nigra* and *C. arvense* in August. *Rubus fructicosus* was also frequently visited in early August and *S. palustris* in late August.

Plant-pollinator interactions differed between habitats (Fig. 3). Networks in arable fields, intensive grasslands and woodlands and their edges (i.e. coniferous and deciduous) were simple with low numbers of pollinators recorded on few plant species. Pollinators in hedgerows mainly foraged on *Cirsium* spp. at the hedge base rather than on woody plants within the hedgerow. In open scrub, interactions were dominated by late flowering species (i.e. *Centaurea nigra*, *Cirsium* spp. and *Succisa pratensis*). Riparian buffer strips and road verges had the most complex plant-pollinator interaction networks. In buffer strips key forage plants included both early (e.g. *Symphytum x uplandicum*) and late (*C. nigra* and *S. palustris*) flowering species; whereas in road verges most interactions occurred on late flowering species (e.g. *C. nigra* and *C. arvense*).

3.2. Drivers of community structure

Annual variation was only detected for area of flowers and hoverfly abundance (Table 2). Such variation is, however, outside the scope of this study.

3.2.1. Floral resources

3.2.1.1 Impact of habitat

Highly significant *Habitat* effects were detected for all flower response variables and these effects were detected in models conducted on the full and reduced (i.e. for the six key habitats: road verges, riparian buffer strips, open scrub, rough grassland and intact and sparse hedgerows) data sets (Tables 2 and 3, Fig. 4). Open scrub, riparian buffer strips and road verges had the highest percentage cover of flowers and the richest, most diverse floral assemblages, with road verges having the highest cover and most diverse assemblages of any of the surveyed habitats. Arable fields, intensive grasslands and coniferous woods had the most impoverished floral assemblages.

3.2.1.2 Consistency of habitat effects across sampling periods

Focussing on the six key habitats, significant *Habitat* and *Sampling period* interactions were only detected for flower species richness (Table 3, Fig. 5). Habitats with high concentrations of flowers therefore provide consistently dense floral assemblages throughout the season. Seasonal trends in flower species richness, however, differed between habitats. Flower species richness in open scrub and riparian buffer strips peaked in July and then declined from July to late August. In road verges richness did not decline until late August.

3.2.2. Insect Pollinators

3.2.2.1 Impact of floral resource variables

In models fitted to the full data set and the six key habitats, abundance, richness and diversity of all pollinator taxa showed a strong positive relationship with floral resource variables (i.e. *Area of flowers* and *Flower species richness*: Table 2, Table 3). Effects of *Flower species richness* were significant when tested after *Area of flowers* indicating pollinators benefitted not just from a greater abundance of flowers but also from richer assemblages. Floristic richness was particularly important for hoverfly response variables and for bumblebee species richness.

3.2.2.2 Impact of habitat

Models fitted to the full data set indicated significant effects of *Habitat* for all pollinator response variables (Table 2, Fig. 4) and, with the exception of butterfly abundance, these effects were still detected for models fitted to the six key habitats (Table 3). Irrespective of taxa, pollinator assemblages in intensively managed agricultural habitats (i.e. arable and intensive grassland fields) and woodlands (i.e. both deciduous and coniferous) were impoverished (i.e. low abundance, richness and diversity). Road verges and riparian buffer strips were the most important (i.e. in terms of abundance, richness and diversity) habitats for bumblebees and hoverflies and alongside open scrub were also important for butterflies (Fig. 4). Utilisation of hedgerows, woodland edges and rough grassland differed across taxa (Fig. 4).

Sequential tests in models in which floral resource variables were tested before and after *Habitat* were utilised to explore if significant *Habitat* effects were solely the

consequence of differences in floral resources observed between habitats. For all butterfly and hoverfly response variables and bumblebee abundance, models conducted on the full data set found significant *Habitat* effects when floral resource variables were tested before *Habitat* indicating *Habitat* effects were not purely driven by differences in floral resources (Table 2). For models restricted to the six key habitats including floral resource variables before *Habitat* resulted in significant *Habitat* effects only being retained for butterfly diversity. Differences in habitat utilisation for all other response variables were therefore largely driven by differences in floral resources observed between the six key habitats (Table 3).

3.2.2.3 Consistency of habitat effects across sampling periods

Focussing on the six key habitats (Tables 3 & A.3, Fig. 5) significant *Habitat* and *Sampling period* interactions were detected for all hoverfly response variables and for bumblebee abundance and diversity. Seasonal trends therefore differed across habitats for these response variables.

Hoverfly abundance and species richness only increased over the full sampling period in road verges and buffer strips. This increase was most apparent in road verges between early and late August when abundances more than trebled. For hoverfly richness there was no evidence of seasonal differences in habitat utilisation over and above those attributed to floral resources; for hoverfly abundance, however, seasonal differences in habitat utilisation could not solely be attributed to differences in floral resources.

Bumblebees in road verges and riparian buffer strips increased from June to July, whereas, in intact hedgerows an increase did not occur until early August. Sequential tests indicated that this *Habitat* x *Sampling period* effect could not be solely attributed to differences in floral resource variables (Table 3). Bumblebee assemblages in road verges and buffer strips were particularly diverse in early August with diversity indices trebling between June and early August; a much greater magnitude of increase than in other habitats. This appeared to be largely due to differences in floral resource variables.

4. Discussion

The importance of semi-natural habitats in providing resources for insect pollinators is well documented (Garibaldi et al., 2011; Kennedy et al., 2013). This is, however, one of the first studies to determine the relative contribution that different habitats (i.e. both semi-natural and agricultural) make to the provisioning of foraging resources for pollinators and additionally explores how this changes over time (Mandelik et al., 2012; Williams et al., 2012). Seasonal trends in floral species richness differed across habitats indicating that their relative profitability as foraging habitats changed. Indeed, temporal variation in habitat utilisation was observed for bumblebees and hoverflies. Seasonal trends in habitat utilisation did not, however, always reflect trends in floristic richness. Temporal variation in habitat utilisation is likely to be dependent not only on the abundance and richness of floral assemblages, but also on the plants making up these assemblages, their peak blossoming periods and additional resources habitats offer.

396 Landscape diversity could influence resource availability through a variety of
397 mechanisms (Fig. 1). Different habitats may stabilise resources at the landscape
398 scale by providing resources at different times (Mandelik et al., 2012; Williams et al.,
399 2012). They may increase the variety of resources to meet the requirements of a
400 greater diversity of species (Shackelford et al., 2013). Finally, different habitats could
401 provide the variety of resources a species requires at a particular point in time (e.g.
402 nectar-rich and pollen-rich flowers) or at different lifecycle stages (e.g. food-plants for
403 butterfly larvae and nectar-rich flowers for adults) (Kremen et al., 2007).
404
405 *4.1. The role different habitats play in the provisioning of floral resources*
406 Pollinators (i.e. butterflies, bumblebees and hoverflies) had strong positive
407 relationships with floral resources (Kohler et al., 2008; Potts et al., 2009; Scheper et
408 al., 2013) and were influenced by both flower abundance and richness with richness
409 being particularly important for hoverflies and bumblebees (Potts et al., 2003).
410 Intensively managed agricultural habitats were devoid of flowers and pollinators were
411 rare in these habitats. Semi-natural habitats are therefore crucial to conserving
412 pollinators in intensive agricultural landscapes (Kennedy et al., 2013; Scheper et al.,
413 2013).

414 Semi-natural habitats differed in the floral resources they offered and this was
415 strongly linked to habitat utilisation by pollinators (Kennedy et al., 2013; Mandelik et
416 al., 2012; Williams et al., 2012). Woodlands typically provided dense, shaded
417 habitats with impoverished floral and pollinator assemblages. Deciduous woodlands
418 may, however, be undervalued as transect walks underestimate pollinators foraging
419 in the canopy and surveying was not conducted during spring when trees can
420 provide early season resources (Baude et al., 2016). Nonetheless, their

impoverished floral assemblages during summer indicate that they need to be complemented by other habitats to ensure resource continuity throughout the season. Of the habitats surveyed, road verges, riparian buffer strips and open scrub had the most abundant and rich floral assemblages indicating their potential value to pollinators (Cole et al., 2015; Noordijk et al., 2009; van Sway et al., 2006). These were key habitats for butterflies, with road verges and buffer strips also being important for bumblebees and hoverflies.

Semi-natural habitats with high numbers of flowers tended to maintain flower abundance throughout the season. Seasonal trends in floristic richness, however, differed thus indicating seasonal variation in their relative value as foraging habitats (Mandelik et al., 2012; Williams et al., 2012). For mobile pollinators, maintenance of floral species richness in road verges later in the season may counteract declines in other key habitats during this period helping to stabilise resources at the landscape scale. Sharp increases in the abundance of hoverflies in road verges late in the season supports the concept that pollinators track resources at the landscape scale altering their foraging pattern in response to the relative availability of resources across habitats (Jha and Kremen 2013; Mandelik et al., 2012; Williams et al., 2012). Seasonal trends in habitat utilisation were not, however, solely accounted for by differences in floral resources. Habitat utilisation will also be influenced by the profitability of plant species present, their peak blossoming periods and additional resources habitats offer. Pollinators switched forage plants in response to temporal changes in availability of key plant species and pollinator occurrence in a habitat was strongly linked to the presence of nectar-rich species such as *Cirsium* spp. and *C. nigra* (Dicks et al., 2002; Pywell et al., 2011; Baude et al., 2016).

445 Our findings support the theory that pollinators respond to resource availability at the
446 landscape scale (Carvell et al., 2012; Jha and Kremen, 2013; Kohler et al., 2008;
447 Holland et al., 2015). We cannot, however, rule out that temporal differences in
448 habitat utilisation were the result of species turnover (i.e. species specific to certain
449 habitats differing in their seasonal peaks) or population responses (i.e. pollinator
450 abundances increasing disproportionately in habitats where resources are plentiful)
451 (Scheper et al., 2013). Exploration of how surrounding landscape composition
452 influences the spatial distribution of pollinators in specific habitats provides an
453 important avenue for future research.
454
455 Habitats differ in the flower species present, indicating habitat diversity increases
456 floral species richness at the landscape scale. Structurally different flower species
457 provide a greater array of foraging niches supporting a greater diversity of pollinator
458 functional groups with flower and pollinator traits coming into play (Fontaine et al.,
459 2005; Richardson et al., 2016; Somme et al., 2015). The main visitors to the delicate
460 open flowers of the *Apiaceae* family were short-tongued hoverflies. Species with long
461 mouthparts (e.g. the bumblebee *B. hortorum* and hoverfly *R. campestris*) preferred
462 deep flowers (e.g. *Stachys* spp.*, Symphytum x uplandicum*) and these species were
463 more abundant in habitats where such flowers were abundant (i.e. road verges and
464 buffer strip). As long-tongued species can exploit different resources to short-
465 tongued species, they may reduce interspecific competition by selectively foraging in
466 habitats where flowers with deep corollas are abundant (Harmon-Threatt and
467 Ackerly, 2013).
468

469 Flower species differ in the rewards they offer and pollinator visitation is influenced
470 by the quantity of nectar and pollen and its chemical composition (Potts et al., 2003;
471 Somme et al. 2015; Richardson et al. 2016). Bumblebees prefer sugar-rich nectar
472 (Cnaani et al. 2006) and pollen selection is based on protein content and
473 composition of amino acids (Somme et al., 2015; Harmon-Threatt and Kremen,
474 2015). Bumblebees visited different flowers to collect nectar and pollen (e.g. nectar
475 from *C. nigra* and *Cirsium* spp. and pollen from *Filipendula ulmaria*). Butterflies
476 visited a restricted number of nectar-rich species (i.e. *C. arvense* and *C. nigra:* Dicks
477 et al., 2002; Pywell et al., 2011; Baude et al., 2016). Hoverflies and bumblebees
478 typically visited a wider range of flowers with the species visited differing between
479 habitats depending on their floristic assemblages. *Helophilus pendulus*, a relatively
480 ubiquitous hoverfly species, predominately foraged on *C. arvense* and *R. repens* in
481 hedgerows and *C. arvense, C. nigra* and *H. sphondylium* in road verges.
482
483 Habitat effects were not solely attributed to differences in floral resources. Across
484 taxa, sunlight appeared to be important with pollinators rarely being recorded in
485 shaded locations such as farm woodlands. In addition to the presence of nectar-rich
486 flowers, butterflies are also require shelter and larval food plants (Holland et al.,
487 2015; Potts et al., 2009; Pywell et al., 2011) and key butterfly habitats (i.e. open
488 scrub, buffer strips and road verges) typically provided all these resources. Linear
489 features (e.g. riparian field margins and road verges) can provide insect flight paths
490 (Cranmer et al., 2012) and later in the season habitat for patrolling male bumblebees
491 (Goulson, 2010) and lekking hoverflies (Sutherland et al., 2001).
492
493 *4.2. Management implications*

Semi-natural habitats differ in the resources they offer which changes over the season. Management should be targeted at improving habitats that are unprofitable to pollinators (e.g. including late-flowering woody plants in hedgerow mixes and creating woodland clearings) and ensuring profitable habitats (e.g. road verges, open scrub and riparian buffer strips) are sympathetically managed - especially during periods of peak utilisation. For example, to avoid widespread resource depletion, the mowing of road verges should be staggered (e.g. by cutting one side of a verge at a time) and avoided during late summer when road verges are particularly profitable foraging habitats.

Mobile pollinators appeared to respond to floral resource availability at the landscape scale actively selecting habitats to meet requirements (Jha and Kremen, 2013; Kennedy et al., 2013; Mandelik et al., 2012). Maintaining landscape heterogeneity and improving the quality of semi-natural habitats will increase resource diversity and continuity. In the study area agri-environment spending focusses on measures to reduce diffuse pollution associated with intensive livestock grazing. Buffer strips are consequently common whereas alternative agri-environmental measures (e.g. wildflower margins or species rich grasslands) are rare. Regionally targeting agri-environment funding to meet local objectives could result in landscape simplification with implications for insect pollinators and biodiversity as a whole (Benton et al., 2003).

A range of semi-natural habitats support pollinators including those managed by private land owners and local authorities. Pollinator conservation therefore requires a landscape-scale approach involving multiple stakeholders and policy sectors. Large-

519 scale conservation initiatives are difficult to implement as they require co-operation
520 between stakeholders (Adams et al., 2016) who often have different perspectives on
521 potential benefits gained (i.e. in this case pollination services: Hein et al., 2006).
522 Pollinator conservation may therefore be particularly challenging to achieve in areas,
523 such as the study catchment, where insect pollinated crops are not grown
524 commercially and the value of pollination services is restricted to maintaining semi-
525 natural habitats.
526
527 **5. Conclusions**
528 Semi-natural habitats provide important foraging resources for insect pollinators in
529 intensive grassland catchments. The relative value of these habitats to pollinators
530 changes seasonally in response to the availability of key floral resources. The large
531 spatiotemporal nature of this study supports the concept that pollinators dynamically
532 use different semi-natural habitats to meet their resource requirements throughout
533 the season. Maintaining landscape heterogeneity and improving the quality of semi-
534 natural habitats has an essential role to play in conserving insect pollinators and the
535 ecosystem services they provide.
536
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543

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Tables

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Table 1. Description of the twelve habitats surveyed including information on their vegetation structure and management. Photographic representation of the habitats is provided in Fig. A.1.

Habitat	*Description*
Arable	Intensively managed wheat or barely receiving high inputs of agrochemicals.
Intensive grassland	Intensively managed productive ryegrass *Lolium perenne* swards grazed by livestock and/or cut for silage.
Rough grassland	Extensively grazed semi-natural grasslands containing a diversity of grass and *Juncus* spp.
Open scrub	Extensively grazed naturally regenerated scrub habitat with areas of more open herbaceous vegetation.
Riparian buffer strip	Unmanaged naturally regenerated vegetation adjacent to and running parallel with a watercourse.
Coniferous wood	Densely planted coniferous woodland with little or no vegetation at ground level.
Coniferous wood edge	Ecotone between coniferous woodland and intensively managed grassland field.
Deciduous wood	Unmanaged semi-natural broadleaved woodland with dense canopy and shrub/vegetated understorey.
Deciduous wood edge	Ecotone between semi-natural deciduous woodland and intensively managed grassland field.
Intact hedgerow	Primarily *Crataegus monogyna* and *Fagus sylvatica* hedgerow compactly structured without significant gaps.
Sparse hedgerow	Primarily *C. monogyna* and *F. sylvatica* hedgerow with many large gaps (i.e. >4m).
Road verge	Vegetated strip adjacent to a road consisting of a mown outer herbaceous edge and inner scrub.

Table 2. Statistical tests from GLMMs and LMMs fitted to the full data set for flower and pollinator (i.e. bumblebees, butterflies and hoverflies) response variables to test for effects of *Habitat*. For pollinator response variables effects of floral resource variables were also tested with *F*-statistics being derived from sequential tests with floral resource variables tested before (bottom) and after (top) *Habitat*. The direction of significant effects for *Area of flowers* and *Flowering plant species richness* were positive. Numerator and ranges for denominator degrees of freedom (which vary in mixed models for different response measures as they are based on estimated variance components) are provided.

	Fixed Effect	Area/ Abundance	Species richness	Shannon
Flowers	*Year*$_{(1,20\text{-}312)}$	13.0***	3.8	0.9
	Sampling period$_{(3,305\text{-}345)}$	17.8***	17.1***	8.1***
	Year x Sampling period$_{(3,305\text{-}345)}$	4.1**	2.6	1.9
	Habitat$_{(11,56\text{-}65)}$	22.2***	17.7***	19.4***
Bumblebees	*Year*$_{(1,11\text{-}296)}$	0.2	0.1	0.8
	Sampling period$_{(3,298\text{-}321)}$	24.3***	8.8***	8.1***
	Year x Sampling period$_{(3,305\text{-}312)}$	8.4***	7.0***	2.0
	Habitat$_{(10,54\text{-}64)}$	8.3***	5.6***	8.7***
		3.2**	1.8	1.8
	Area of flowers$_{(1,330\text{-}366)}$	14.9***	4.3*	3.7
		39.0***	18.7***	45.0***
	Flower species richness$_{(1,253\text{-}357)}$	10.4**	13.8***	17.7***
		37.2***	37.6***	46.0***
Butterflies	*Year*$_{(1,44\text{-}284)}$	1.1	3.4	0.7
	Sampling period$_{(3,348\text{-}361)}$	67.6***	14.2***	6.1***
	Year x Sampling period$_{(3,344\text{-}366)}$	4.5**	2.3	2.2
	Habitat$_{(11,58\text{-}74)}$	7.3***	11.5***	8.8***
		4.5***	6.6***	3.1**
	Area of flowers$_{(1,324\text{-}411)}$	8.4**	8.5**	6.2*
		29.6***	56.1***	62.2***
	Flower species richness$_{(1,87\text{-}342)}$	9.3**	7.2**	6.0*
		18.2***	13.8**	11.9***
Hoverflies	*Year*$_{(1,30\text{-}298)}$	6.7*	0.4	0.0
	Sampling period$_{(3,345\text{-}353)}$	71.2***	39.9***	24.8***
	Year x Sampling period$_{(3,344\text{-}357)}$	8.6***	3.8*	2.5
	Habitat$_{(11,60\text{-}79)}$	12.0***	12.4***	13.3***
		4.1***	4.5***	3.2**
	Area of flowers$_{(1,398\text{-}409)}$	5.1*	10.4**	11.3***
		45.6***	62.6***	102.7***
	Flower species richness$_{(1,\ 163\text{-}257)}$	24.2***	28.6***	19.8***
		70.7***	64.1***	38.7***

***P<0.001, **0.001≤P<0.01, *0.01≤P<0.05

Table 3. Statistical tests from GLMMs and LMMs fitted to the reduced data set (i.e. for the six key habitats) for flower and pollinator response variables to test for effects of *Habitat* and *Habitat x Sampling period*. For pollinator response variables effects of floral resource variables were also tested with *F*-statistics being derived from sequential tests with floral resource variables tested before (bottom) and after (top) *Habitat* and *Habitat x Sampling period*. The direction of significant effects for *Area of flowers* and *Flowering plant species richness* were positive. Numerator and ranges for denominator degrees of freedom (which vary in mixed models for different response measures as they are based on estimated variance components) are provided.

	Fixed Effect	Area/ Abundance	Species richness	Shannon
Flowers	*Year*$_{(1,20\text{-}144)}$	14.8***	1.8	1.1
	Sampling period$_{(3,141\text{-}155)}$	15.2***	16.2***	9.7***
	Year x Sampling period$_{(3,141\text{-}155)}$	5.4**	3.0*	1.6
	Habitat$_{(5,32\text{-}33)}$	13.2***	11.2***	9.4***
	Habitat x Sampling period$_{(15,141\text{-}155)}$	1.7	2.0*	1.3
Bumblebees	*Year*$_{(1,12\text{-}172)}$	0.6	0.2	0.7
	Sampling period$_{(3,146\text{-}157)}$	16.8***	6.1***	6.6***
	Year x Sampling period$_{(3,147\text{-}154)}$	4.6**	3.8*	1.5
	Habitat$_{(5,26\text{-}38)}$	6.1***	5.4**	6.9***
		2.0	1.2	1.1
	Habitat x Sampling period$_{(15,146\text{-}152)}$	1.8*	0.9	1.7*
		1.7*	0.9	1.4
	Area of flowers$_{(1,164\text{-}178)}$	9.1**	3.8	1.5
		19.1***	10.3**	11.5***
	Flower species richness$_{(1,123\text{-}172)}$	3.1	5.6*	6.3*
		15.1***	19.6***	29.5***
Butterflies	*Year*$_{(1,22\text{-}186)}$	2.5	1.2	0.3
	Sampling period$_{(3,\ 145\text{-}186)}$	47.7***	11.7***	6.8***
	Year x Sampling period$_{(3,145\text{-}186)}$	5.3**	2.6	1.7
	Habitat$_{(5,\ 26\text{-}186)}$	2.5	3.1*	4.5***
		1.8	2.0	2.6*
	Habitat x Sampling period$_{(15,146\text{-}186)}$	1.5	0.5	1.2
		1.0	0.6	1.4
	Area of flowers$_{(1,174\text{-}186)}$	3.2	9.1**	5.8*
		11.3***	15.0***	14.7***
	Flower species richness$_{(1,\ 76\text{-}186)}$	2.9	2.8	6.5*
		5.0*	2.1	5.1*
Hoverflies	*Year*$_{(1,25\text{-}157)}$	9.2**	0.5	0.1
	Sampling period$_{(3,146\text{-}156)}$	50.5***	29.2***	27.7***
	Year x Sampling period$_{(3,146\text{-}155)}$	5.6**	2.8*	2.1
	Habitat$_{(5,27\text{-}54)}$	7.2***	5.3**	4.3**
		1.3	0.6	0.8
	Habitat x Sampling period$_{(15,143\text{-}151)}$	2.5**	2.0*	2.7***
		2.3**	1.7	2.1*
	Area of flowers$_{(1,176\text{-}181)}$	1.8	2.6	5.0*
		19.6***	20.0***	24.0***
	Flower species richness$_{(1,75\text{-}135)}$	7.7**	10.3**	8.4**
		23.4***	21.5***	17.1***

***P<0.001, **0.001≤P<0.01, *0.01≤P<0.05

Figure legends

Graphical Abstract: The role that habitat diversity plays in the provisioning of resources for insect pollinators at the landscape scale.

Fig. 1. Conceptual model highlighting the potential processes driving pollinator populations at the landscape scale. This provides a framework for the investigation that outlines how these processes are explored, both directly and indirectly.

Fig. 2. Spatial overview of the study catchment indicating the location of the 84 sampling sites (i.e. seven sites per habitat class). Insert provides a high resolution aerial image of a subset of these sites.

Fig. 3. Plant-pollinator bipartite interaction graphs indicating effects of *Habitat* on the relative frequency of pollinator visits to different flower species. Graphs are based on data summarised across all *Sampling periods* for each for the twelve *Habitats*. To facilitate interpretation all plant-pollinator interactions capturing a single pollinator visit to a single plant species in a specific *Habitat* were omitted. Plants are displayed on the left of the graph with pollinators on the right. Width at the pollinator end represents the relative frequency that a specific plant pollinator interaction was observed in a specific *Habitat*. See Tables A.1 and A.2 for full Latin names.

Fig. 4. Influence of *Habitat* on (a) flowering plants, (b) bumblebees, (c) butterflies and (d) hoverflies. For a specific transect the raw data were summarised first over *Year* (for transects sampled in both years) and then over *Sampling period*, the means and SEMs were then derived over all transects within a *Habitat* category. Means not sharing the same letter are significantly different (pairwise comparison using the false discovery rate method: $p<0.05$).

Fig. 5. Influence of *Habitat* and *Sampling period* interactions on Flower richness, bumblebee abundance and diversity and hoverfly abundance, diversity and richness. These graphs are based on data for the six key habitats. For transects sampled in both years data were first summarised over *Year*, and then for each *Sampling period* the means were derived over all transects within a *Habitat* category. To ease interpretation SEMs are not displayed on these graphs.

Figure 1

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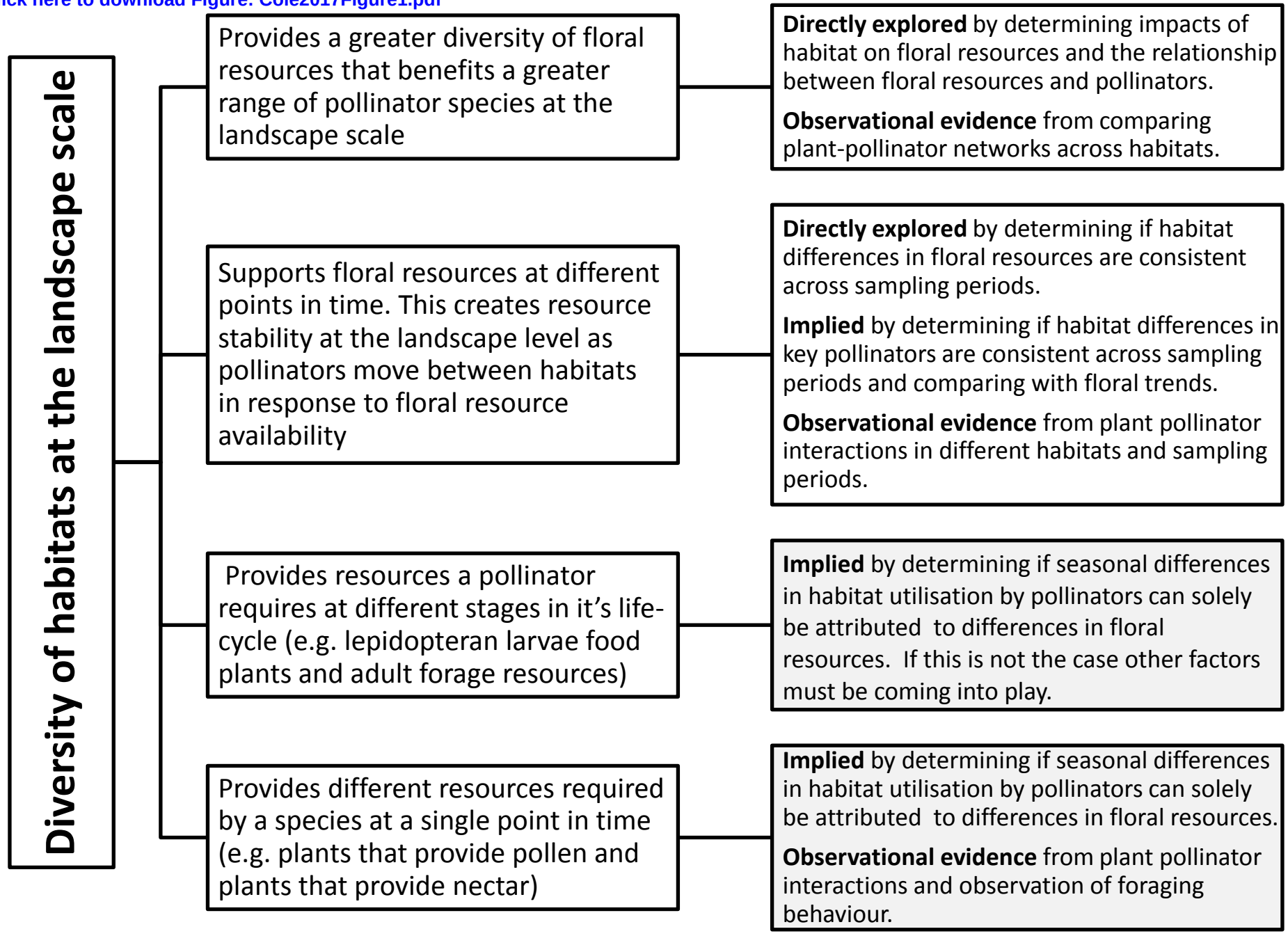

Figure 2

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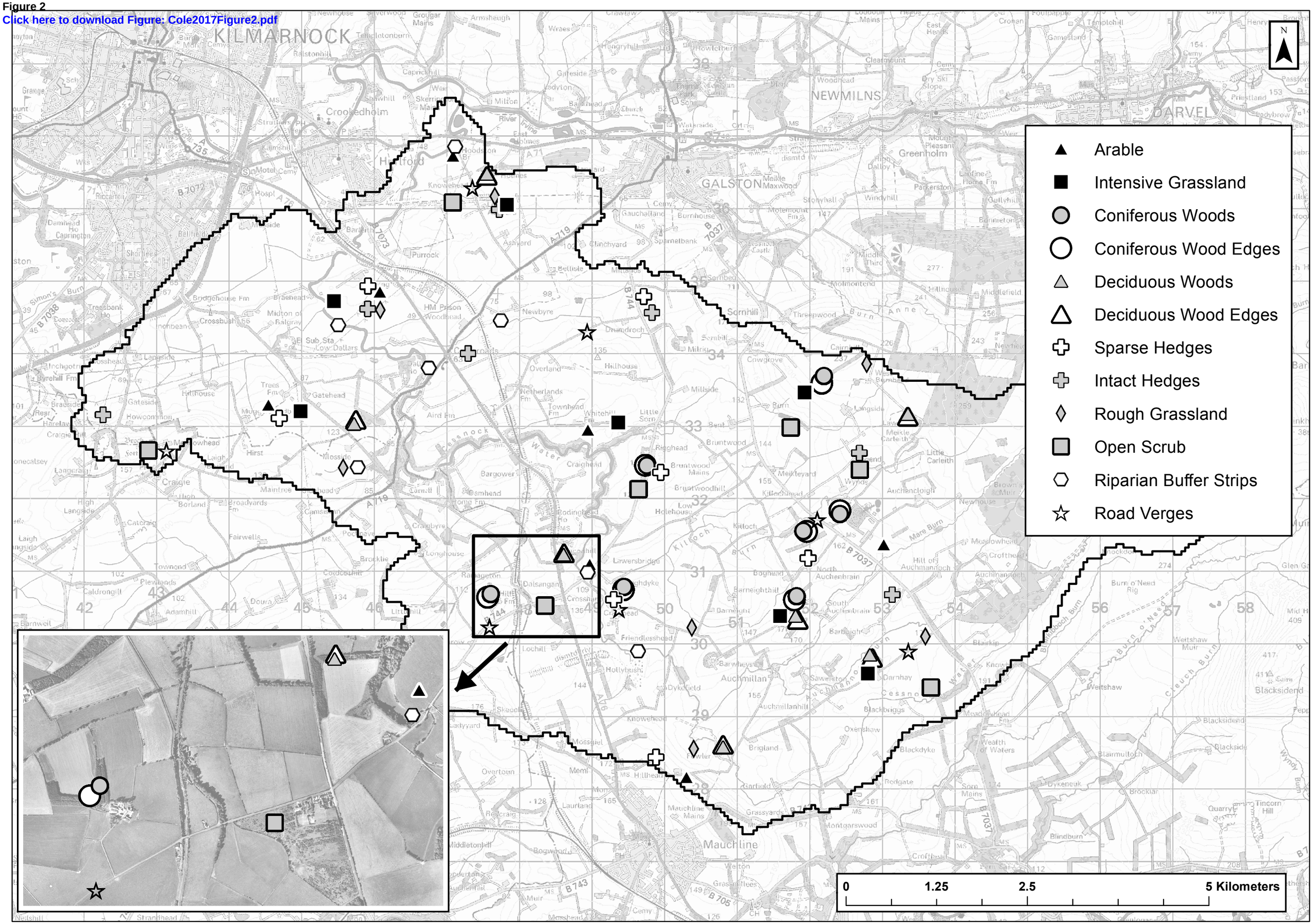

Figure 3

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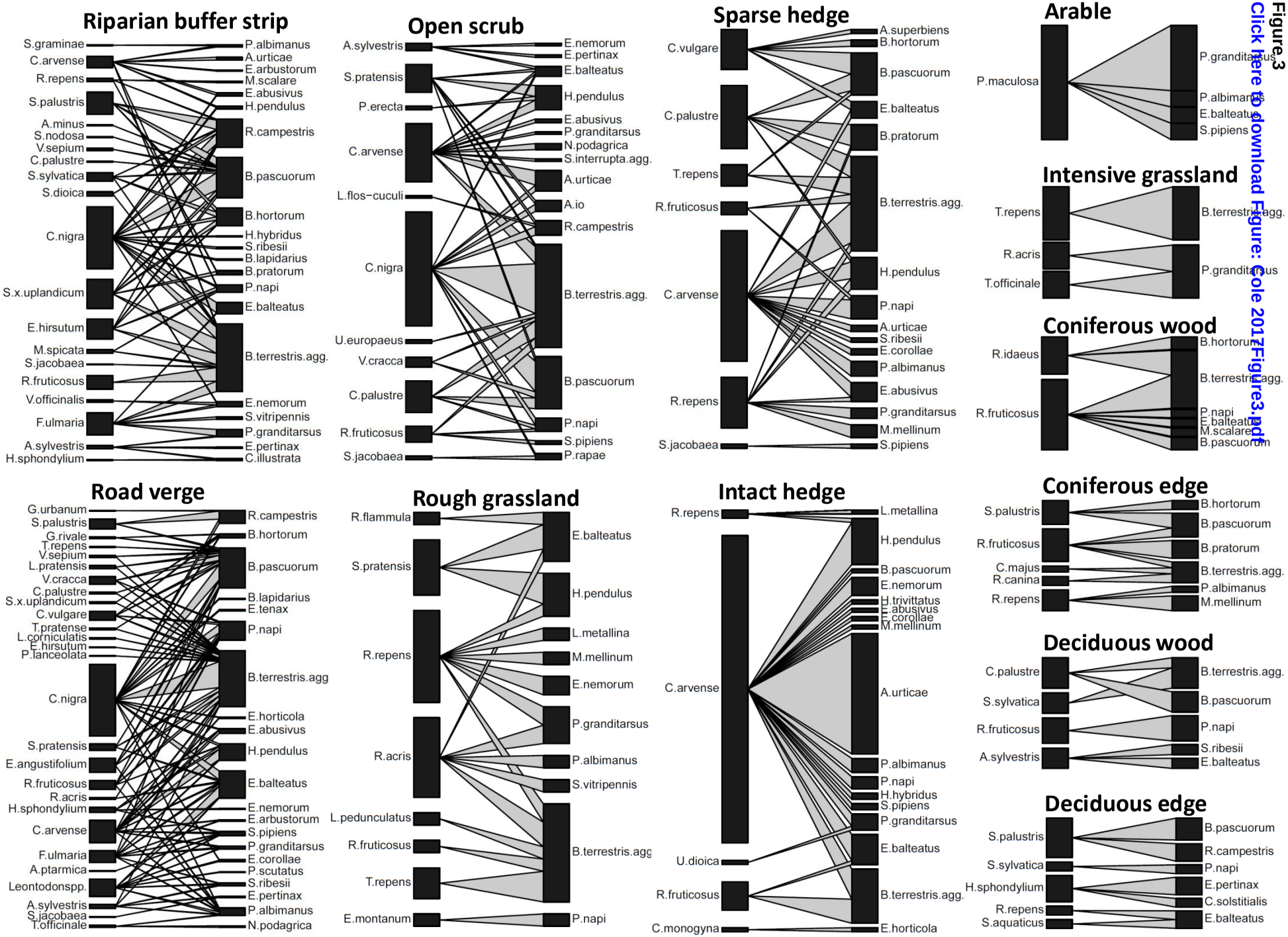

Figure 4

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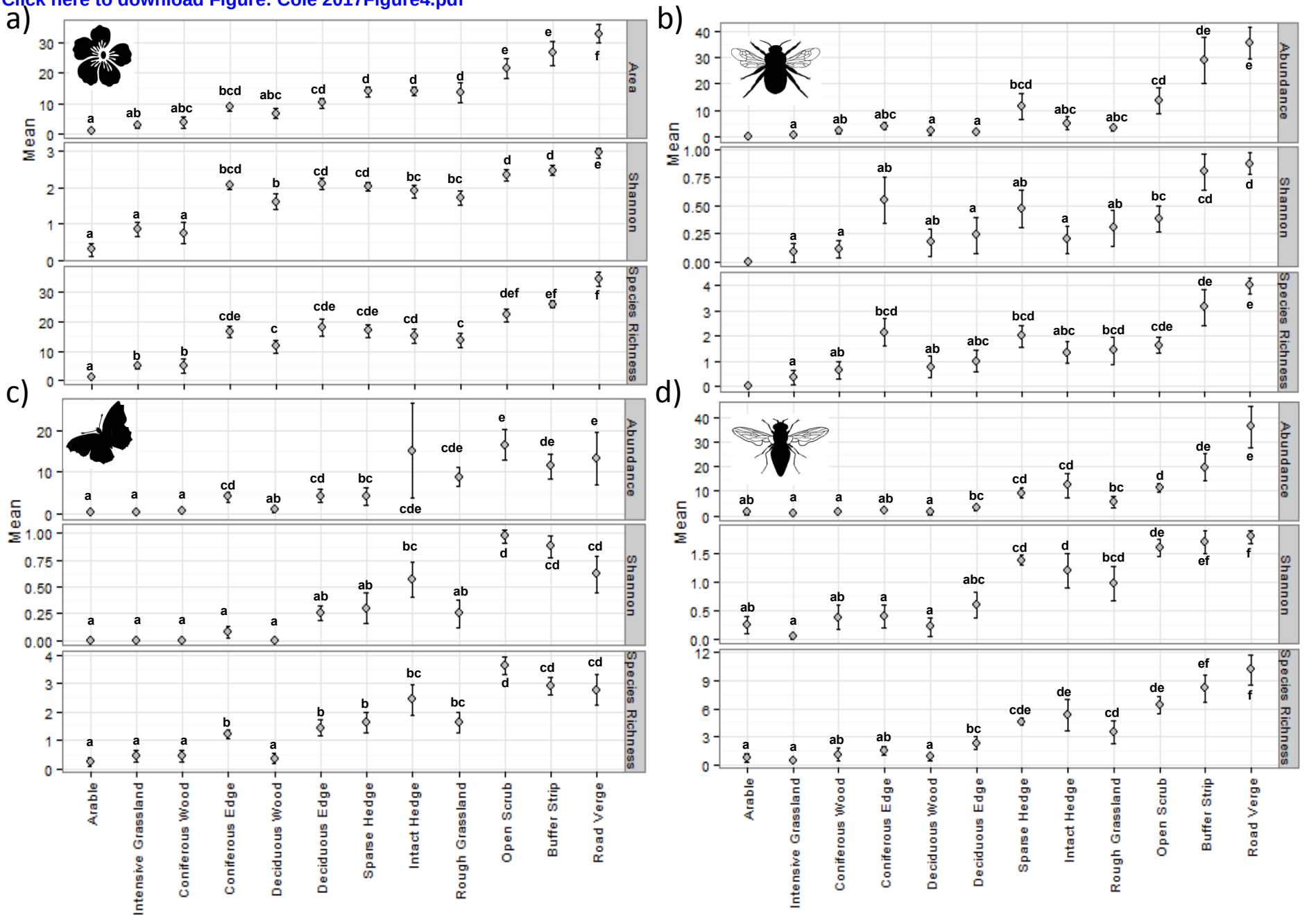

Figure 5

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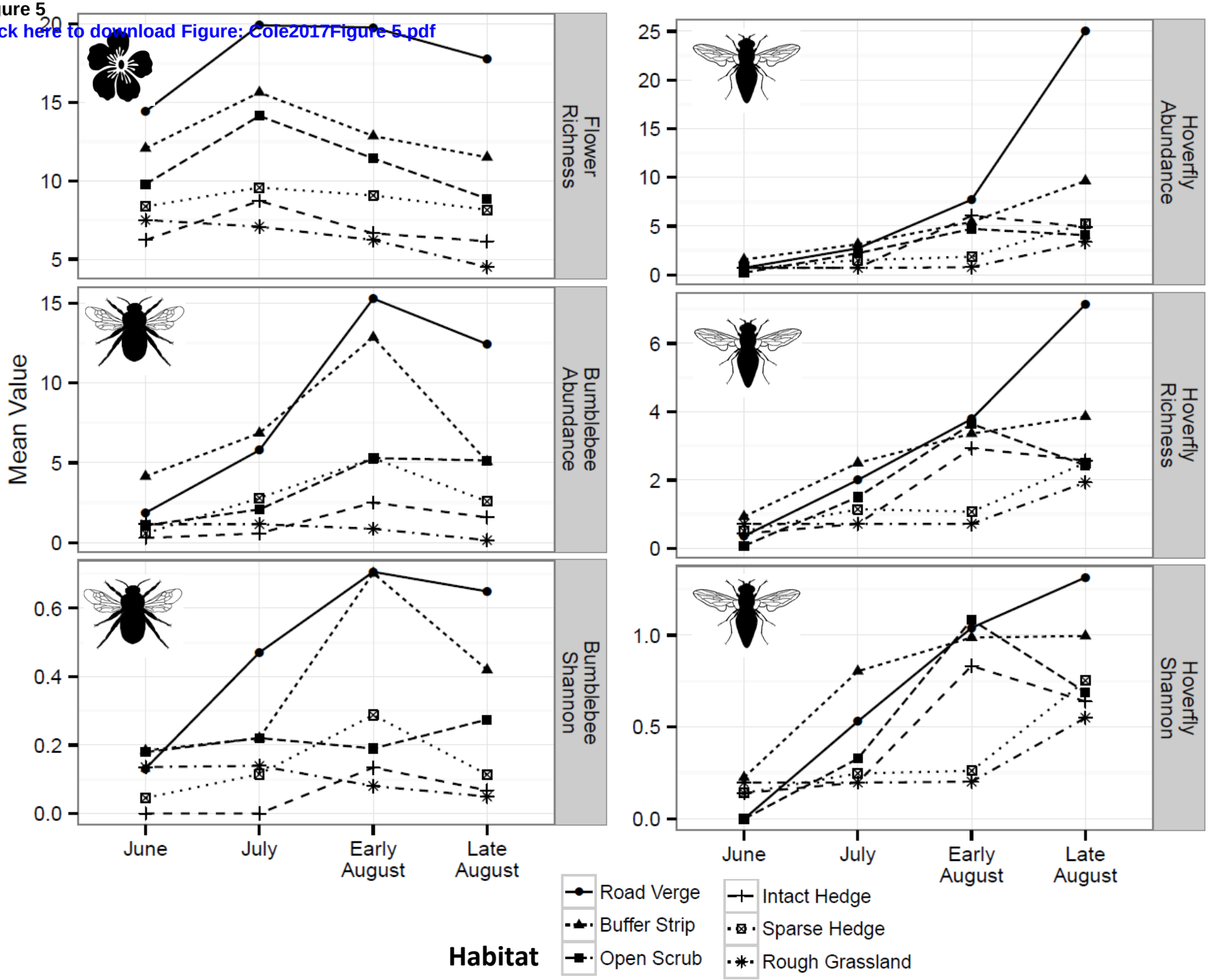

Supplementary Tables

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Supplementary Fig.A1

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Supplementary Fig.A2

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Supplementary Fig.A3

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